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ORIGINAL ARTICLE

Macroinvertebrate biodiversity patterns during primary succession in manmade ponds in north-eastern Spain

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ABSTRACT

The aim of this work was to evaluate the primary succession of manmade ponds by studying the temporal patterns of the pond biodiversity metrics. We surveyed the macroinvertebrate community, the water and the sediment of 19 manmade ponds of different ages (from 1 to 22 years) located at reclaimed opencast coal mines in north-eastern Spain. This study showed an increase of biodiversity with pond age: the oldest ponds showed higher complexity and more rare taxa than the youngest ponds, while the taxonomic richness did not change. These results highlighted the need for using a wide range of biodiversity metrics. Moreover, our results suggest that post-mining landscapes could be limiting environments for the evolving macroinvertebrate community because pond age explained less of the biodiversity variance than the environmental characteristics. The changes found in water and sediment during this time were not reflected in changes in biodiversity, and the levels of biodiversity in our study area were lower than those of restored or manmade ponds of similar ages.

Key words: Pond age, taxonomic distinctness, rarity, richness, chrono-sequence approach, opencast coal mines.

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INTRODUCTION

Succession (defined here as the process of change in species composition in an ecosystem over time) is a key process related to the functioning of the ecosystem (Margalef, 1968; Odum, 1969; Gutiérrez and Fey, 1980). Therefore, we think that a deep knowledge about succession is essential to understand ecological processes. Recent studies have shown high pond contribution to biodiversity and geochemical cycles among other ecological functions (Oertli *et al.*, 2002; Williams *et al.*, 2004; Zedler and Kercher, 2005). Although ponds have been neglected by scientific community, the number of constructed ponds increase and they were a perfect scenario to study succession trajectories (De Meester *et al.*, 2005; Céréghino *et al.*, 2008; Boix *et al.*, 2012; Ruhí *et al.*, 2013). Moreover, a deeply knowledge about temporal patterns of the community is required in order to improve the success in restoration projects, which have as objective restore the structure of the expected natural community and to enhance biodiversity (Gallardo *et al.*, 2011; Ruhí *et al.*, 2012; Moreno-Mateos *et al.*, 2012).

The knowledge about the basic processes driving primary succession in wetlands remains limited (Noon, 1996), particularly with respect to changes in the faunal community (Batzer *et al.*, 2006). Moreover, most successional studies have been based on temporary wetlands and therefore strictly analyzed secondary succession processes (Lake *et al.*, 1989; Boix *et al.*, 2004). Manmade ponds form excellent model systems for analyzing the primary succession process because pond construction allows to study community composition from the onset of habitat creation (Velasco *et al.*, 1993; Flory and Milner, 2000; Matthews *et al.*, 2009). So, to study manmade ponds allows to improve primary succession knowledge and offers new information to support to design most efficient ecosystems in relation to their construction objectives.

Biodiversity, studied as community composition, is a suitable community metric for studying primary succession because it is important in maintaining the biogeochemical cycles and functioning of the ecosystem (Loreau *et al.*, 2001; Hooper *et al.*, 2005). However, empirical studies describing how biodiversity changes over time in manmade ponds are scarce and most of these studies focused on changes in taxonomic richness. Traditional ecological papers hypothesized that there is an increase in biomass and taxonomic richness during succession (Odum, 1969; Gutiérrez and Fey, 1980; Legendre *et al.*,1985). Some authors verified an increase in richness during the initial colonization of newly created ponds (Barnes, 1983; Ruhí *et al.*, 2009, 2012; Marchetti *et al.*, 2010). However, after the initial changes in biodiversity, the rate of acquisition of new species tends to decline within a few years from the onset of succession (Barnes, 1983; Fairchild *et al.*, 1999; Proctor and Grigg, 2006; Marchetti *et al.*, 2010), indicating an equilibrium in the

number of species, as predicted by the theory of island biogeography (MacArthur and Wilson, 1967; Whittaker and Fernández-Palacios, 2007). Moreover, over longer time scales, unimodal responses may also be present (Rosenzweig, 1992; Hansson *et al.*, 2005), while other authors found no pattern in long-term studies regarding biodiversity when using taxonomic richness (Gee and Smith, 1995; Spieles *et al.*, 2006). Nevertheless, no single index alone is a suitable surrogate to represent overall biodiversity community dynamics (Warwick and Clarke, 1995; Wilsey *et al.*, 2005; Heino *et al.*, 2007). Taxonomic richness alone may not represent all of the biodiversity aspects of the community and therefore has been over used as a measure of biodiversity (Bilton *et al.*, 2006; Gallardo *et al.*, 2011). Other metrics, such as taxonomic distinctness and rarity, that take into account complementary aspects of the concept of biodiversity, should be considered (Warwick and Clarke, 1995). These two biodiversity aspects illustrate different but complementary techniques of inferring community characteristics (Heino *et al.*, 2007; Gascón *et al.*, 2009). For example, it has been suggested that pioneering taxa are taxonomically highly related, and lower values of taxonomic distinctness are expected at the initial phases of succession (Ruhí *et al.*, 2009). Moreover, it has been reported that as succession progresses, colonization is mainly driven by the erratic arrival of dispersers with lower dispersal abilities (Ruhí *et al.*, 2013). Therefore, at later successional phases, an increase in the rarity values of macroinvertebrate assemblages is expected due to the erratic arrivals of such taxa that also may produce increased taxonomic unevenness. Accordingly, we expected that taxonomic distinctness and rarity change during primary succession.

To analyze primary succession an extensive temporal range of data is needed, in other case only colonization phase could be considered (Zedler and Callaway, 1999; Fairchild *et al.*, 2000; Ruhí *et al.*, 2012). However, obtain long-term series of data usually is a difficult issue and to overcome this problem, space-for-time approaches has frequently been adopted (*e.g.*, Barnes, 1983; Fukami and Wardle, 2005; Bloechl *et al.*, 2010). The present study focused on macroinvertebrate organisms from manmade ponds constructed at different time-periods during reclamation activities at opencast coal mines. Consequently, the studied ponds have different ages (from 1 to approx. 22 years old). Ponds were located in post-mining landscapes reclaimed with similar techniques, shared similar substrate and were affected by similar climatic conditions which made them appropriate for the use of the chronosequence approach for studying primary succession (Majer and Nichols, 1998; Walker *et al.*, 2010). Thus, our main objective was to analyze the temporal patterns of biodiversity during primary succession using complementary biodiversity metrics. We considered several questions: i) Is biodiversity changing over time? ii) Are temporal changes in biodiversity related to environmental changes (and if so, to which factors)? iii) Is pond age the main factor explaining the variation in biodiversity? To answer these questions, we studied the biodiversity of the macroinvertebrate community and the environmental characteristics (water, sediment and landscape) of a set of manmade ponds constructed at different times during opencast coal mining reclamation. Due to the particular characteristics of the study site, we included a fourth question: iv) Is the biodiversity of manmade ponds constructed in post-mining landscapes similar to the biodiversity of manmade ponds constructed in other environmental conditions?

METHODS

Study site

The current study was conducted in north-eastern Spain (Teruel Province), which is characterized by a continental Mediterranean climate. The manmade ponds sampled in this study (Fig. 1) were constructed during the reclamation process of several coal mines. In this region, coal mines worked the same coal seam with similar extraction methods and followed comparable reclamation patterns. The manmade ponds were all created for the same purpose, to manage the water runoff produced in the reclaimed mines to avoid contaminating natural ecosystems but not with the specific objective of enhancing the biodiversity values of the region. Following our study site knowledge, we selected 19 manmade ponds, covering an age range of 22 years, that were as similar as possible in their physical characteristics. Thus, the manmade ponds have endorheic basins and are isolated from watercourses, except for two ponds connected by a small stream. All of the manmade ponds are permanent and have similar water level fluctuations as well as oval shapes and their size were among 0.2 and 5 ha (with a size mean of 1.5 ha). *Typha* sp. (among the only macrophytes found in the manmade ponds) grows at high-density in the banks of the ponds, except for three ponds where macrophytes were scarce or absent. No natural ponds formerly existed in the river basin where the mines are located.

Sampling and sample processing

Two surveys were conducted: one in the spring and one in the summer of 2009. In each pond, samples of macroinvertebrates, water and sediment were collected, and pond and landscape characteristics were measured.

Macroinvertebrate sampling

Macroinvertebrate collections were restricted to shallow sites (<1 m deep) located in the littoral of the man-

made ponds. One integrated sample from the major mesohabitats (emergent plants, bottom and water column) was collected from each pond with a 250-µm-mesh hand-net using the kick-and-sweep sampling technique. Sampling was considered complete when no new taxa were found by visual observation. The macroinvertebrate samples were preserved in 4% formalin. The samples were washed through nested sieves in the laboratory and the collected fauna was sorted under a stereomicroscope and identified mostly to the genus level (except for the Oligochaeta and Diptera).

Water characteristics

Dissolved oxygen, temperature, conductivity and pH were measured *in situ* using portable probes (WTW® Multiline P4, Weilheim, Germany). Water samples were collected at a depth of 15-20 cm and brought to the lab for further analyses. Chlorophyll-*a* was analyzed by spectrophotometry. Alkalinity (mg L^{-1}) was determined by pH potentiometric automatic titration with 0.004 N H_2SO_4 (Metrohm®, Herisau, Switzerland). Water samples were filtered through pre-ashed glass-fibre filters. Total suspended solids and total suspended organic matter were calculated by filter and burned filter weight differences, respectively. Total dissolved nitrogen (mg L^{-1}) and non-purgeable organic carbon (mg L^{-1}) were determined by catalytic combustion at high temperature using a Multi-N/C 3100 analyzer (Analytik Jena®, Jena, Germany). In addition, we determined total dissolved phosphorus and 10 dissolved trace metals (mg L^{-1}), Al, As, Cd, Cr, Cu, Fe, Mn, Ni, Pb and Zn, using Inductively Coupled Plasma Optical Emission Spectrometry (ICP-OES iCAP6300Duo; Thermo Fisher®, Waltham, MA, USA). Analyses performed in the laboratory followed the standard methods of the American Public Health Association (APHA *et al.*, 1992). All the materials used for metal analysis were soaked in 10% HNO3 (Sastre *et al.*, 2002).

Sediment characteristics

One composite sample of sediment was collected in the littoral zone of each pond. Sediment pH and conductivity (µS cm^{-1}) were measured in a solution of 10 g of fresh sediment dispersed in deionised water (pH: 2.5:1 g mL^{-1}, conductivity: 5:1 g mL^{-1}) after shaking for 30 min. The collected sediments were air dried and sieved into fractions. For the <2-mm sieved sediment, we calculated the particle-size by laser-diffraction analysis (Syvitski, 2007) using a Mastersizer 2000® particle size analyzer

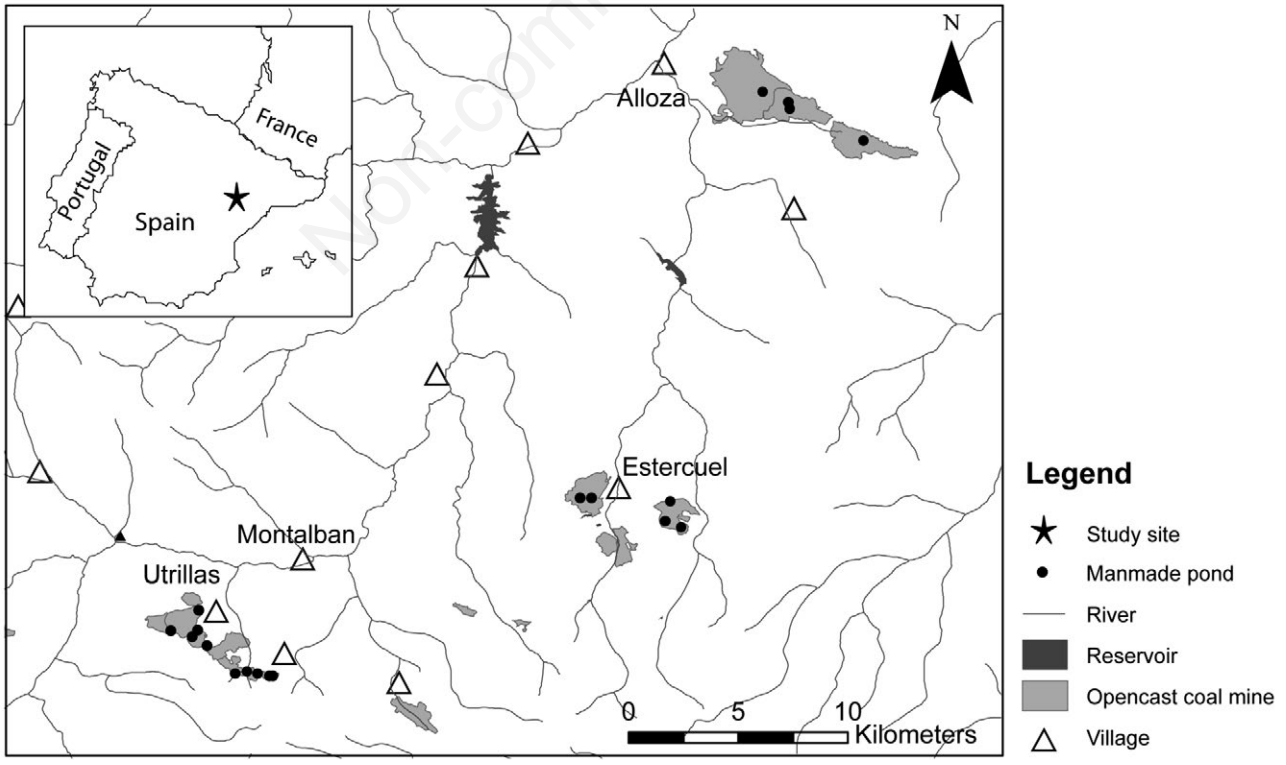

Fig. 1. Study site and pond locations.

(Malvern Instruments, Malvern, UK). We obtained the percentage of sand, thick silt, thin silt and clay. The <2-mm fraction was also used to determine total carbon (%), total inorganic carbon (%) and total sulphur (%) using an elemental analyzer (LECO SC-144DR; Leco Instruments®, St. Joseph, MI, USA). Total organic carbon (%) was calculated by the difference between total carbon and total inorganic carbon. Total nitrogen (%) was determined using an elemental analyzer (Variomax® CN). The <63-µm fraction was used to determine total phosphorus (mg kg^{-1} DW) and total heavy metals (mg kg^{-1} DW): Al, As, Cd, Cr, Cu, Fe, Mn, Ni, Pb and Zn. The phosphorus and metals were microwave extracted (Speedwave MWS-3, Berghof, Germany), following the methods of the US Environmental Protection Agency (EPA, 2007) and then determined using ICP-OES following the American Public Health Association methods (APHA *et al.*, 1992).

Landscape characteristics

Pond and landscape characteristics were estimated with geographic information systems (ArcGis 9.3.1 Esri) and fieldwork observations. We calculated pond area (m^2), pond littoral slopes (%), pond basin slope (degrees), vegetated pond littoral area (m^2), distance to nearest pond (m), distance to nearest river (m), the numbers of ponds in a 1000-m buffer and the number of rivers in a 1000-m buffer.

Data analysis

Biodiversity metrics

As the macroinvertebrate sampling effort was not comparable among ponds, to characterize the macroinvertebrate community, we calculated four biodiversity metrics that did not require abundance estimations: rarefied richness, average taxonomic distinctness, variance of taxonomic distinctness and index of faunal originality as the rarity index. Biodiversity metrics were calculated for each pond in each season.

Species richness increases with sample size, and differences in richness may be caused by sampling differences (Oksanen *et al.*, 2009). Rarefaction is a method for comparing species richness between treatments, after standardization, to account for sampling effort. Therefore, rarefied richness (RR) minimizes the differences between the sampling effort, collection conditions and organism abundances (Gotelli and Colwell, 2001). In this case, RR was standardized according to the minimum number of invertebrate collected in one sample using the *rarefy* function that was available in the *Vegan* package (Oksanen *et al.*, 2009), which is a statistical package that provides tools for descriptive community ecology developed for the R statistical software (R Core Team, 2012). Taxonomic distinctness metrics consider the relatedness of species in each sample incorporating the phylogenetic relationships among taxa (Clarke and Warwick, 1998). We considered two taxonomic distinctness metrics, Average taxonomic distinctness (AvTD) and Variance in taxonomic distinctness (VarTD) because they are not sensitive to variation in sampling effort and are calculated with presence-absence data (Clarke and Warwick, 1998). AvTD is the mean path length between any two randomly chosen taxa traced through a Linnaean or phylogenetic classification of the full set of documented taxa (Clarke and Warwick, 1998) and is a proxy of the taxonomic relatedness of the taxa encountered in the analyzed assemblage. In comparison, VarTD is the variance of these pairwise path lengths and reflects the unevenness of the taxonomic tree (Clarke and Warwick, 2001). AvTD and VarTD were calculated with PRIMER v6 using a setting of 100, which is the longest path length in taxonomy. The path lengths between the different taxonomic levels of the classification tree (based on standard Linnaean hierarchical classification) were considered equal. Six taxonomic levels (genus, family, order, class, phylum and kingdom) were considered in the aggregation file. Finally, we calculated the rarity of the macroinvertebrate community through the Index of Faunal Originality (IFO), which only needs presence-absence data and is, therefore, independent of the taxonomic abundance. IFO was calculated for each manmade pond according to Puchalski (1987):

$$IFO = \frac{\sum_{i=1}^{S}(1/M_i)}{S}$$

where M is the total number of samples in which taxon i occurs (total number of manmade ponds in which a particular taxon appears) and S is the total number of taxa in the corresponding sample (the total number of taxa in the manmade pond for which the index is calculated). The theoretical maximal value of the index is 1, indicating that none of the taxa found in one pond were recorded in another pond.

Statistical analysis

The ponds were grouped into four age categories (Pond Age Categories, hereafter PAC) for statistical analysis: PAC1, 1–5 years (5 ponds); PAC2, 6–10 years (5 ponds); PAC3, 11–15 years (4 ponds); and PAC4, 16-22 years (5 ponds).

To explore biodiversity changes across the PACs, we used linear mixed models (LMM), with PAC as the fixed effect and season as a random effect. The inclusion of season in the random part of the model allowed us to control pseudo-replication problems due to sampling each pond in two different seasons (Hurlbert, 1984). We performed the linear mixed models using the *lme* function integrated in the *nlme* package (Pinheiro *et al.*, 2012) designed for R statistical software (R Core Team, 2012). A ln-transfor-

mation of IFO was needed to improve the error fitness to a normal distribution.

The biodiversity levels of the manmade ponds constructed in the reclaimed opencast coal mines were compared with data from other studies undertaken with manmade or restored wetlands and ponds of different ages. We selected nine studies Barnes (1983), Hov and Walseng (2003), Solimini *et al.* (2003), Lancaster *et al.* (2004), Spieles *et al.* (2006), Proctor and Grigg (2006), Ruhí *et al.* (2009), Marchetti *et al.* (2010), and Ruhí *et al.* (2012) that considered some of the biodiversity metrics used in this study (RR, AvTD, VarTD and IFO) or offered taxonomic lists that allowed their calculation. Note than in Ruhí *et al.* (2009), we only considered the data for permanent manmade ponds.

To determine whether the environmental characteristics of the manmade ponds vary over time, we used two discriminant analyses (DA), one for water (water-DA) and another for sediment (sediment-DA) characteristics. DA is a multivariate method that generates a series of discriminant functions based on linear combinations of predictor variables that provide the best possible discrimination (or maximal separation) between pre-established groups (Hair *et al.*, 2005; Corstanje *et al.*, 2009). Therefore, DA allows for the statistical determination of significant differences in water and sediment characteristics among the four PACs and thus determines whether environmental characteristics change significantly over time. These analyses were carried out using SPSS 19 for Windows (SPSS Inc., Chicago, IL, USA). Before the analysis, all variables, except pH, were log(x+1) transformed. To reduce multi-collinearity problems in the DA, we excluded from the analysis those highly associated metrics (of water and sediment datasets) based on Spearman rank correlations (if $P<0.01$ and $r_s \geq 0.7$; Myers 1986). In such cases only one of the metrics was retained.

Finally, we performed variation partitioning analyses to quantify the proportion of biodiversity variability explained by the four groups of predictors considered in this study: PAC, water, sediment and landscape datasets. This analysis breaks down and quantifies the explained variation in the dependent variables (biodiversity metrics) as pure (or unique) and shared (or joint) effects of a set of predictors (age and environmental datasets). Thus, we distinguished three type of effects: pure (the variation explained by only one dataset without considering the effects the other datasets included in the analysis), shared (the variation explained by one dataset and its interaction with other datasets included in the analysis) and global (the variation explained by one dataset and its interaction with all the datasets included in the analysis). For more information about variation partitioning see Borcard *et al.* (1992), Heikkinen *et al.* (2005), Peres-Neto *et al.* (2006) and Wang *et al.* (2011). The variation partitioning analyses is integrated in the *varpart* function as part of the *Vegan* package (Oksanen *et al.*, 2009) available for the R statistical software (R Core Team, 2012). One variance partitioning analysis was performed with each biodiversity metric: RR, AvTD, VarTD and IFO. Before performing variation partitioning, we identified the predictor variables within each dataset (water, sediment and landscape) having independent impacts on the biodiversity metric to only include the environmental variables that significantly explain the variability of each metric in each analysis. We identified these variables by the use of the 'rand.hp' function, which is a randomization routine integrated into the 'hier.part' package (MacNally and Walsh, 2004) available for the R statistical software (R Core Team, 2012) and which focuses on the analysis of the variance partition of a multivariate data set. This analysis showed the independent contribution toward the explained variance in a multivariate dataset. The results of 'rand.hp' were expressed as Z-scores and the statistical significance was based on the upper 95% confidence limits ($Z \geq 1.65$; MacNally 2002).

RESULTS

Biodiversity changes across ponds of different ages

Although RR did not show any significant response through successional stages (*i.e.*, PAC), the other three biodiversity metrics did. AvTD, VarTD and IFO significantly increased with pond age (Fig. 2), indicating that as ponds mature, the macroinvertebrate assemblages that inhabit them increase in rarity (IFO), average taxonomic distinctness (AvTD) and unevenness of the taxonomic tree (VarTD). The faunal list by PAC is shown in Tab. 1.

Water and sediment characteristics among pond age categories

The variables included in the water-DA selected after determining the correlations were: chlorophyll-a concentration, pH, conductivity, alkalinity, non-purgeable organic carbon, total dissolved nitrogen, total dissolved phosphorus, Al, As, Cr, Cu and Ni. The variables used in the sediment-DA were: pH, total inorganic carbon, total organic carbon, total sulphur, thin silt fraction, clay fraction, As, Cr, Cu, Fe, Mn, Ni and Zn.

The discriminant analysis of the water characteristics showed that only the first of the three discriminant functions (DF) was significant in differentiating PACs based on the χ^2 test ($P<0.05$). The first DF showed a high canonical correlation with PAC ($\rho=0.827$) and accounted for 67.2% of the explained variance. The first three DFs were significant for sediment characteristics ($P<0.05$). All three had a significantly high canonical correlation coefficient with PAC ($\rho=0.916$, 0.834 and 0.801), accounting from 56.2% of the explained variance for the first DF to 19.2%

for the third DF. Both water-DA and sediment-DA clearly discriminated youngest ponds (PAC1) from the rest of the ponds (Fig. 3 A,B). The differences in water characteristics (Fig. 3A) were related to total nitrogen content, which was the variable better correlated to the first DF (r=0.453), indicating that younger ponds had higher nitrogen concentrations.

The first DF obtained with the sediment dataset (Fig. 3B) was positively correlated with total organic carbon (r=0.361), total sulphur (r=0.221) and several heavy metals (iron r=0.250; arsenic r=0.244; and chromium r=0.208), while the pH (r=-0.286) and total manganese content (r=-0.236) were negatively correlated. Thus, youngest ponds had less total organic carbon and metal content than older ponds. Both DAs indicated that the youngest ponds (PAC1) were different in their environmental characteristics compared to the other three PACs. Consequently, the main environmental changes were detected when comparing youngest ponds (from 0 to 5 years old) with older ponds (from 6 to 22 years old), in which environmental conditions remained similar (Fig. 3 A and B).

Factors explaining the biodiversity variability

The variation partitioning results (Tab. 2), performed after variable selection (see Tab. 3 to identify selected variables after the randomization routine) showed that the

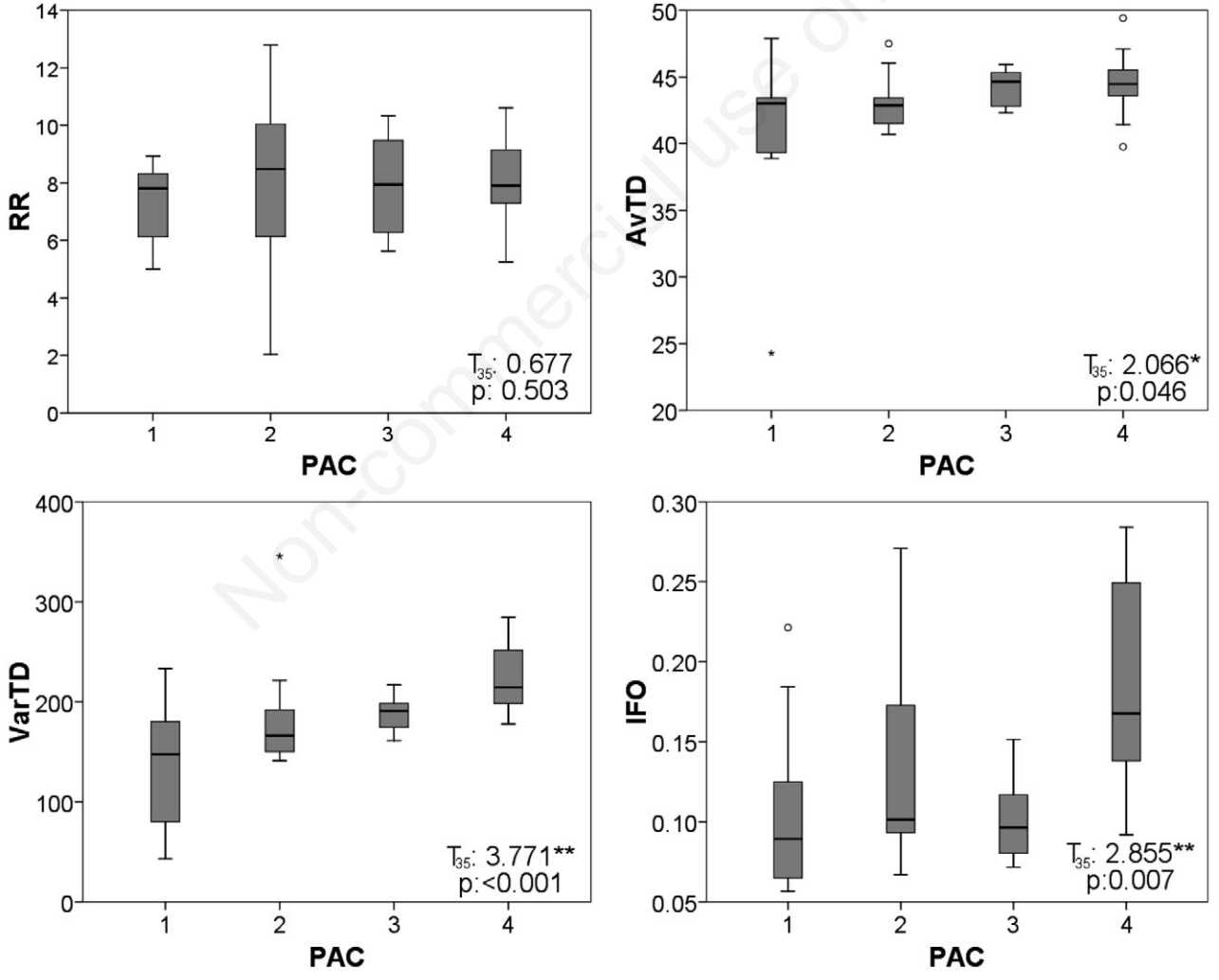

Fig. 2. Long-term biodiversity trends. The values of each biodiversity metric (RR, rarefied richness; AvTD, average taxonomic distinctness; VarTD, variation in taxonomic distinctness; IFO, index of faunal origin) are represented by the pond age category (PAC). Spearman correlations and p-values are shown. Box-plots symbols: dark grey box, interquartile range (IQR: Q3-Q1); black horizontal line within the dark grey box, median (Q2); upper whisker, upper (Q3+1.5IQR); lower whisker, lower (Q1-1.5IQR); circle, mild outlier: asterisk, extreme outlier.

proportion of variation explained by pond age, water, sediment and landscape datasets varied with respect to the biodiversity metrics analyzed. Overall, the environmental characteristics and pond age explained a higher proportion of the variation in the taxonomic distinctness metrics (more than 50%) than in RR and IFO (less than 40%). This indicates that the age and the environmental characteristics of the ponds contributed significantly, but to a lesser extent, to the observed variation in taxonomic richness and abundance of rare taxa. Our results showed that the observed variability in biodiversity metrics was not purely explained by pond age. When also accounting for the shared variability of pond age with the other environmental variables (*i.e.*, the global pond age effect), pond age significantly explained VarTD and IFO variability (Tab. 2). Water (pure and global) significantly explained some of the variability in RR and VarTD and also explained some of the variability in IFO, when considered in relation to the other data sets (global effect). Sediment was significant for AvTD, VarTD and IFO only with re-

Tab. 1. Taxonomic distribution of macroinvertebrates found in each pond age categories.

		Pond age category						Pond age category			
Group	Taxa	1	2	3	4	Group	Taxa	1	2	3	4
Coleoptera	*Donacia*	+	+	+	-	Diptera	Eriopterini	-	-	-	+
	Dryops	+	-	-	-		*Pericoma*	-	-	-	+
	Acilius	+	+	-	+		*Tenatocera*	+	-	-	-
	Bidessus	+	+	-	-		*Nemotelus*	-	-	-	+
	Coelambus	+	+	-	-		*Odontomyia*	-	+	-	+
	Copelatus	+	+	-	-		*Oxycera*	-	+	-	+
	Eretes	+	+	-	+		*Tipula*	-	-	-	+
	Graptodytes	+	+	+	+	Ephemeroptera	*Cloeon*	+	+	+	+
	Hydroglyphus	+	+	-	-		*Procloeon*	-	+	+	+
	Hydroporus	+	+	-	-		*Caenis*	+	+	+	+
	Hygrobia	-	+	-	-		*Ephemera*	+	+	+	+
	Hygrotus	-	+	-	-		*Thraulus*	-	+	-	+
	Hyphydrus	+	+	+	-	Hemiptera	*Corixa*	+	+	+	+
	Ilybius	+	+	+	+		*Cymatia*	+	+	+	+
	Laccophilus	+	+	+	+		*Micronecta*	+	+	+	+
	Meladema	-	-	-	+		*Sigara*	-	+	-	-
	Scarodytes	-	-	-	+		*Gerris*	+	+	+	+
	Yola	+	+	-	+		*Mesovelia*	-	-	+	-
	Limnius	+	-	-	-		*Naucoris*	+	+	+	+
	Gyrinus	-	+	-	-		*Anisops*	+	-	+	-
	Haliplus	+	+	+	+		*Notonecta*	+	+	+	+
	Helophorus	-	+	+			*Plea*	+	+	+	+
	Limnebius	-	-	-	+	Megaloptera	*Sialis*	-	-	-	+
	Berosus	+	+	+	+	Odonata	*Anax*	+	+	+	+
	Hydrochara		+	-	-		*Aeshna*	-	+	-	+
	Helochares	+	+	+	-		*Gomphus*	-	+	-	+
	Laccobius	-	-	-	+		*Onychogomphus*	-	+	-	-
	Hydrochus	-	-	+	-		*Coenagrion*	+	+	+	+
	Noterus	-	+	+	+		*Ceriagrion*	-	+	-	-
	Hydrocyphon	-	-	-	+		*Ischnura*	+	+	+	+
Diptera	Ceratopogonidae	+	+	+	+		*Lestes*	+	+	+	+
	Orthocladiinae	+	+	+	+		*Sympecma*	+	+	+	+
	Chironomini	+	+	+	+		*Crocothemis*	+	+	+	+
	Tanypodinae	+	+	+	+		*Libellula*	-	-	+	-
	Tanytarsini	+	+	+	+		*Orthetrum*	+	+	+	+
	Anopheles	+	+	+	+		*Sympectrum*	+	+	+	+
	Culex	-	+	-	+		*Platycnemis*	-	-	-	+
	Culiseta	-	-	-	+	Trichoptera	*Ecnomus*	-	-	+	+
	Dixella	-	+	+	+		*Allotrichia*	+	+	+	-
	Dolichopodidae	+	+	-	+		*Setodes*	+	-	+	+
	Hydrellia	+	-	-	-		*Micropterna*	-	-	-	+
	Scatella	+	+	-	+		*Agrypnia*	-	-	-	+
	Dicranomyia	-	+	+	-		*Plectrocnemia*	+	-	-	-
	Helius	-	+	+	+	Oligochaeta	Tubificidae	+	+	+	+
	Pilaria	-	-	-	+						
	Rhypholophus	+	-	-	-						

spect to the global effect and, similarly, landscape only had significant global effects in explaining the variability of RR, AvTD and VarTD. In general, the proportion of variation explained by environmental characteristics was higher than the variation explained by pond age for any of the biodiversity metrics tested, indicating a small effect of pond age on biodiversity.

DISCUSSION

Curiously, taxonomic richness, the most widely used index of biodiversity, was the only metric that did not show any significant response when comparing pond age categories. Other studies performed in constructed (Gee *et al.*, 1997) or restored wetlands (Marchetti *et al.*, 2010) of similar life spans (from 0 to 20/25 years in age) also failed to detect a long-term increase in taxonomic richness, although Marchetti *et al.* (2010) detected an increase in richness during the first five years after pond restoration.

This result does not necessarily mean that community composition does not change. Spieles *et al.* (2006) found a change in guild dominance across time, although basic community metrics (richness and abundance) showed no significant differences over a 10-year range. Similarly, the number of taxa in our study did not change significantly, whereas the taxonomic structure of the assemblages and rarity did (Fig. 2). Colonization processes in newly created

Tab. 2. Results of the variation partitioning analysis for the biodiversity metrics with respect to water, sediment, landscape and pond age categories. The proportions of unexplained, pure, global and shared variations are shown for pond age and the other three sets of variables.

		RR	AvTD	VarTD	IFO
Water	Pure	0.12*	0.17	0.20**	0.10
	Global	0.31**	0.51	0.62**	0.20*
Sediment	Pure	-	-0.01	0.04	0.13
	Global	-	0.15*	0.42**	0.29*
Landscape	Pure	0.04	0.03	0.01	-
	Global	0.27**	0.33**	0.39**	-
PAC	Pure	0.00	0.00	0.04	-0.02
	Global	-0.01	0.07	0.27**	0.14**
PAC and water	Shared	-0.03	0.07	0.20	0.09
PAC and sediment	Shared	-	0.08	0.23	0.16
PAC and landscape	Shared	0.00	0.07	0.24	-
Unexplained		0.63	0.47	0.26	0.62

*RR, rarefied richness; AvTD, average taxonomic distinctness; VarTD, variation in taxonomic distinctness; IFO, index of faunal origin; PAC, pond age category. The significance of pure and global effects was tested (*0.05, **0.01); significance tests for the combined effects are not available.*

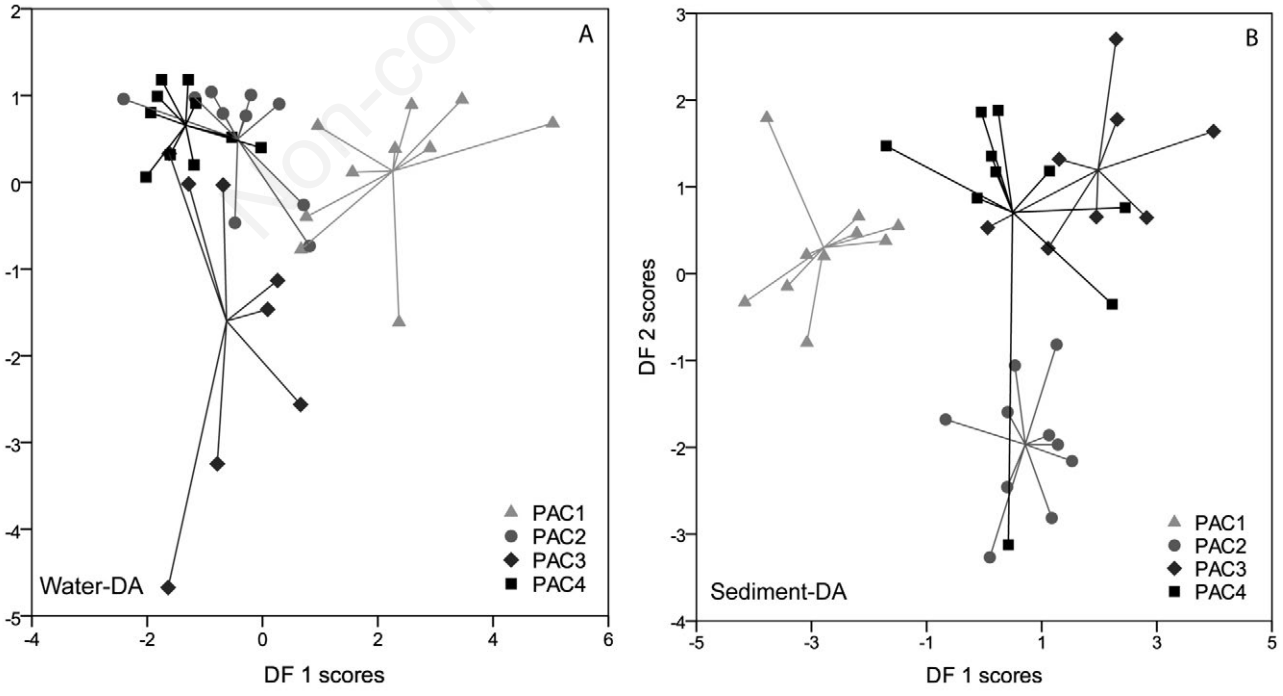

Fig. 3. Scatter plot of the first two functions (DF1 and DF2) of the Discriminant Analysis using water (A) and sediment (B) characteristics to differentiate pond age categories (PAC).

ponds have been suggested to be driven by a few taxonomic groups, and during succession, new taxa arrive, while some pioneering taxa disappear (Layton, 1991; Ruhí *et al.*, 2009). In addition, an increase in the arrival of passive dispersers or active dispersers having lower dispersal abilities over time has been described (Ruhí *et al.*, 2013). Thus, a balance between the arrival and disappearance of taxa may explain the lack of richness differences among pond age categories. Moreover, the increase in AvTD and VarTD suggests that the new taxa arriving in the manmade ponds belong to distant taxonomic groups (because we detected an increase of the phylogenetic distance among taxa, AvTD) and were unequally distributed in the taxonomic tree (because of the increase of VarTD). The significant increase in rare taxa (IFO values) could be due to the erratic arrival of new taxa and it is reasonable to think this also may contribute to the increase in VarTD values.

Despite the positive tendency detected in AvTD, VarTD and IFO over time, we noticed that PAC alone did not significantly explain the biodiversity of manmade ponds. This means that changes that occur over time were not the main source of biodiversity variability in the macroinvertebrate community of the manmade ponds. Indeed, we found a higher importance of environmental characteristics over pond age explaining the biodiversity variability. Moreover, when differences in water and sediment among PAC were found (the environmental characteristics of PAC1 were different from PAC 2 to 4), we did not detect clear differences in biodiversity metrics (Figs. 2 and 3). The lack of synchronization in the changes in pond characteristics and biodiversity, combined with the significant contribution of the landscape features to the explanation of biodiversity variability (*i.e.*, taxonomic distinctness), suggested that local environmental characteristics may play an important role in the macroinvertebrate community configuration. The biodiversity of the manmade ponds constructed in reclaimed opencast coal mines was low compared to other constructed or restored ponds of similar pond ages (Tab. 4). Indeed, the biodiversity in our study showed lower values than other manmade ponds located in post-mining landscapes, as was the case in Moura (Australia). The low biodiversity values combined with the greater environmental than PAC explanation of the biodiversity variability among ponds suggested that the macroinvertebrate community inhabiting the ponds constructed in the reclaimed coal mines of Teruel were constrained by the particular characteristics of the study area. The homogeneity of the pond habitat (*e.g.*, littoral ponds were dominated by *Typha* sp. and ponds had similar sediment texture) may be one important reason for the low biodiversity values because faunal biodiversity is positively correlated with the complexity of the pond habitat (O'Connor, 1991; Pedruski and Arnott, 2011). Moreover, it is possible that the manmade ponds were polluted due to coal mining despite mine reclamation. In fact, several metals showed a relevant contribution to the biodiversity explanation (Tab. 3). These metals may contribute to the low biodiversity values due their negative effects over macroinvertebrate community (Clements, 1994; Van Damme *et al.*, 2008; Iwasaki *et al.*, 2009). Finally, the development of the macroinvertebrate community may have been limited by the recruitment of organisms (Palmer *et al.*, 1996; Brady *et al.*, 2002; Brederveld *et al.*, 2011). No natural wetlands or ponds were

Tab. 3. Variables selected from the three groups of explanatory variables (water, sediment and landscape) for each biodiversity metric introduced in the variation partitioning analyses.

	RR	AVTD	VARTD	IFO
Water	Chlorophyll-a	pH	Chlorophyll-a	Chlorophyll-a
	Suspended organic matter	Non purgueable organic carbon	Non purgueable organic carbon	Dissolved Oxygen
	Total suspended solids	Total dissolved nitrogen	Total dissolved nitrogen	
		Al	Ni	
		Fe	Fe	
		Zn	Zn	
Sediment		Total carbon	Total carbon	Total carbon
		Clay fraction	Clay fraction	Total sulphur
			Conductivity	Total organic carbon
			As	Total nitrogen
				As
				Cr
				Ni
Landscape	Littoral vegetation area	Littoral vegetation area	Littoral vegetation area	
		Pond area	Pond area	
			Numbers of ponds in a 1000-m buffer	

RR, rarefied richness; AvTD, average taxonomic distinctness; VarTD, variation in taxonomic distinctness; IFO, index of faunal origin.

Tab. 4. Biodiversity data collected from several studies on macroinvertebrate communities in constructed or restored ponds. The biodiversity metrics values represent the mean biodiversity of ponds within the age categories considered in the present study.

Site	Studied community	Purpose	Age	Metrics					Reference
				Richness	RR	AvTD	VarTD	IFO	
Teruel (Spain)	Genus	Runoff control in reclaimed opencast coal mines	1 to 5	-	7.3	41.09	138.19	0.11	This paper
			6 to 10	-	8.0	43.20	188.12	0.13	
			11 to 15	-	7.9	44.23	188.24	0.10	
			16 to 22	-	8.0	44.44	223.47	0.18	
California (USA)	Genus	Return degrade wetlands to functional natural ecosystems	1 to 5	23.5	21.3	44.85	253.35	0.34	(Marchetti *et al.*, 2010)
			10	29.0	25.4	44.76	233.60	0.38	
			>20	30.0	23.6	44.66	224.30	0.52	
Catalonia (Spain)	Genus	Habitat and species recovery	1 to 3	-	-	59.91	355.85	-	(Ruhí *et al.*, 2009)
Rome (Italy)	Genus and Family	Wastewater aquaculture treatment	1 to 3	26.0	24.5	49.23	268.23	0.44	(Solimini *et al.*, 2003)
Kalmar (Sweden)	Species	Wastewater airport treatment	1 to 3	22.6	-	66.75	247.13	-	(Ruhí *et al.*, 2012)
		Increase of biodiversity	7	27.5	-	65.90	187.96	-	
			13	11.0	-	75.95	181.49	-	
Moura (Australia)	Family	Pit ponds result of coal mining	0 to 4	14.0	9.3	43.02	289.97	0.19	(Proctor and Grigg, 2006)
			12 and 14	14.7	7.1	40.79	287.07	0.22	
			17 and 22	14.5	8.3	41.41	294.40	0.20	
Central Ohio (USA)	Genus	Wetland mitigation lost	10	23.5	25.5	48.40	184.08	0.53	(Spieles *et al.*, 2006)
Dunfermline (UK)	Genus	Urban drainage treatment ponds	1 to 5	21.6	-	62.86	512.56	0.48	(Lancaster *et al.*, 2004)
Trogstad (Norway)	Genus	Nutrient pollution treatment	1 to 5	24.2	-	39.77	254.85	0.55	(Hov and Walseng, 2003)
Dorset (UK)	Genus	Pit ponds result of clay extraction	1 to 3	29.7	-	45.08	229.63	0.33	(Barnes, 1983)
			15	41.0	-	46.71	286.10	0.42	

RR, rarefied richness; AvTD, average taxonomic distinctness; VarTD, variation in taxonomic distinctness; IFO, index of faunal origin.

found near the coal mines, and the manmade ponds were isolated from water courses. Therefore, the source of macroinvertebrates may be primarily restricted to distant streams. This fact may reduce the probability of colonizing the manmade ponds because the macroinvertebrate community of lotic ecosystems is different and shows lower dispersal abilities than the macroinvertebrates inhabiting lentic ecosystems (Ribera and Vogler, 2000; Marten *et al*., 2006).

Comparing biodiversity values with other studies allow to search for temporal biodiversity patterns among different regions. To perform this comparison, we selected AvTD and VarTD because of their lack of dependence on sampling effort allow for a comparison across studies from different localities or from regions using different sampling methods (Clarke and Warwick, 1998). The AvTD *vs.* VarTD scatter plot (Fig. 4) showed no relationship between biodiversity and pond age when the manmade wetlands and ponds of different study sites were compared. Moreover, neither the geographic area nor the construction objective were determining factors (Tab. 4) similar results were obtained by Ruggiero *et al.* (2008). Therefore, the local conditions of each study appear to be more important for explaining macroinvertebrate biodiversity than the general patterns.

CONCLUSIONS

In summary, this study demonstrated that even constructed ponds located in post mining landscapes and without an enhanced biodiversity purpose showed an increase in almost all of the studied biodiversity metrics over time. The only biodiversity metric that did not in-

Fig. 4. Scatter plot of variation in taxonomic distinctness (VarTD) against average taxonomic distinctness (AvTD) to compare the biodiversity of 10 different study sites in relation to pond age. Data corresponding to table 4 were used.

crease is the metric that is mainly used to assess biodiversity (*i.e.*, richness). This fact highlights the importance of using a range of biodiversity metrics to study the macroinvertebrate community, which agrees with previous studies (Wilsey *et al.*, 2005; Heino *et al.*, 2007; Gascón *et al.*, 2009; Gallardo *et al.*, 2011). Our results suggest that environmental factors better explain the configuration of pond biodiversity than pond age. This fact, coupled with the low biodiversity detected in our study area, suggest that environmental conditions may restrict the number and type of taxa that are able to colonize and become established in manmade ponds and therefore restrict the process of the macroinvertebrate community maturation. However, because biodiversity metrics increased over time (except for rarefied richness) and natural ponds are absent from the studied area, manmade ponds constructed during reclamation activities to control runoff may provide both biological and landscape diversity, at least at a regional scale. The study of manmade ponds is a useful tool to understand the functioning of the increasing number of manmade ponds around the world and also provide new ecological information to guide future pond construction.

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